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ON THE GENETIC ENERGY OF ORGANISMS.*

For several years the conviction has been growing more and more definite in my mind that the fundamental principle in vital phenomena is to be found in variation rather than in heredity. The first time this opinion was definitely expressed in print was in 'Geological Biology' (1894): "Variability is thus assumed to be an inherent characteristic of all organisms, and origin of species has primarily to consider how comparative permanency of characters, and of different sets of characters in different lines of descent, is brought about" (p. 184); and: "The search has been for some cause of variation; it is more probable that mutability is the normal law of organic action, and that permanency is the acquired law," etc. (p. 297). Two years later Professor L. H. Bailey said in his 'The Survival of the Unlike' (1896): "In other. words, I look upon heredity as an acquired character, the same as form or color or sensation is, and not as an original endowment of matter" (p. 23). Perhaps others have published the same conclusion, but, if so, I have not elsewhere seen the point advanced as a scientific proposition.

The conviction was reached on my part through studies in paleontology. As early as 1881 I was struck by the evidence of a

*A paper read before the American Society of Naturalists, December 24, 1897, by Henry Shaler Williams, Yale College, New Haven, Conn.

beginning, adolescence, maturing and old age of races of species in the geological past, advanced by Hyatt and later elaborated so fully by him and others. flected back to the nature of development, which such geological recapitulation seems to imitate, as a process in which the cellular parts of the individuals are undergoing a constant process of varying, and I conceived of the law of recapitulation as an extension of the principle of varying first seen in the cells of the individual to successive organisms. This principle of 'recapitulation,' which was taught by Agassiz, emphasizes at least the wide applicability of variability in organic processes.

I have been testing, in all conceivable ways, the application of this theory to the facts of biology for the past fifteen years, but for only a short time have I been aware of the revolutionary nature of the conception.

As I discover no escape from the essential validity of the proposition, and because of the importance of it for future investigations, and because few biologists with whom I have spoken seem to understand the importance of the problem at issue, it may not be inappropriate to attempt at this time to state the foundation upon which the theory appears to rest.

THE SOURCE OF OUR KNOWLEDGE OF ORGANIC PHENOMENA.

One of the difficulties standing in the way of forming clear and distinct notions of organic phenomena lies in the fact that we are not accustomed to orient them in their exact relationship to the current notions of physical and mathematical science.

When we contemplate a physical body of matter as growing, varying, inheriting, acquiring characters or selecting, the body which performs these acts so far transcends anything which the physicist knows about simple masses of matter, and the performances so far transcend the kind of work he

is accustomed to deal with, that, as a physicist (whatever his opinion may be of biologists), he frankly confesses he has no knowledge in the case. Without attempting any metaphysical discussion, and without stating whether the biologist does or does not know any more than the physicist in the matter, we may join hands with the latter in the belief that if anything is known about them it can be expressed in scientific terms only by an analysis of the observed phenomena in the case.

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In seeking, therefore, for the fundamental characteristic of a living organism we ask, first, how does it differ, phenomenally, from a similar body not organic?

If we consider ultimate chemical or physical constitution we discover no fundamental distinction between a living organism and the same body of dead matter.

The same chemical elements compose them; the same physical properties pertain to each. Even mechanically, it is perhaps impossible to define wherein they differ.

When we observe the functions of the organism we note certain phenomena in the living body not operating in the same body after death; but in all these functions we discover none which are not like those of dead bodies of matter in this respect that a specific amount of equivalent of heatenergy is used in their operations, and the energy used is transformed from some other condition, as in inert matter, and no energy seems to be gained or lost in the process. Thus in the two aspects of constitution and action of the bodies it is difficult, and probably it is impossible, scientifically, to describe any constant point of difference in quality between an organism and a body of matter which is not alive.

There is, however, one point of difference: A living body is constantly changing in its material constitution, while an inert body remains the same. An organism persists in becoming different so long as it lives,

while a mass of matter remains in a state of rest or of uniform direction of motion, except as compelled by some outward force to change that state.

It may be objected, here, that this difference is a subjective one, and has no objective reality, in that a body, of which the substance is undergoing change, cannot be regarded as strictly the same body after as before the change.

If the objection be valid we must still remember that it is such a changing physical body which grows, inherits, acquires characters, etc., that we are studying.

But whether the objection be valid or not, it is essential to keep our attention on the objective reality, the living organism, whatever difficulties we may have subjectively; and the one group of phenomena which the live organism exhibits characteristically is that of becoming different.

It is, then, this distinguishing characteristic of the living body—its becoming different—that constitutes the point of view from which it is believed the true relations of the organism to other physical bodies may be seen.

Most biologists, I suppose, are accustomed to treat of living organisms as if they were simple physical masses of matter exhibiting their peculiar phenomena solely on account of their peculiar organization, including under that term molecular arrangement of the protoplasm as well as molar organization of the body of the individual. This conception involves the hypothesis that the peculiarity of the phenomena is to be accounted for by difference in kind, state, condition or structure of the component matter of the body.

Starting with such a conception, let us examine the phenomena and discover of what they consist.

CLASSIFICATION OF VITAL PHENOMENA.

In order to distinguish the phenomena

of the organism from other phenomena and to restrict our attention, let us call the peculiar visible phenomena of an organism vital phenomena.

Vital Phenomena may be divided into three groups, according to the relation they bear to mode of existence.

- A. When the question is: What organisms are? the phenomena described in the answer are found in the sciences of Botany, Zoology, Anatomy, etc.
- B. When we ask: What do organisms do? the phenomena are described under the names of Physiology, Physiological Chemistry and Psychophysics.
- C. When we ask: What do organisms become? the replies are found in Paleontology, Embryology, Evolution and Psychology.

This third group (C) of phenomena, because they are modes of becoming different and in a peculiar sense arise or are generated, may be called genetic phenomena.

The other two classes (A and B) may be left out of discussion for the present, because their relationships to ordinary physical phenomena are sufficiently distinct and evident.

The Genetic Phenomena of organisms are of, at least, three kinds; they are described under the scientific categories of

C¹ Metabolism,

C2 Development,

and C³ Evolution.

In the phenomena of each of these three categories there are two elements, viz.: (1) a something which preserves its identity and integrity during the phenomena, which may be designated by the symbol x; and (2) a something which arises during the phenomenon and remains as an increment to the first; this may be represented by y.

 C^{l} . In Metabolism x stands for the matter flowing into the organism from without, and constitutes the physical basis of the organic body at any particular moment of its

existence; y is the complex and instable chemical union of the elements, set up in anabolism, which represents a definite quantity of potential chemical energy, that may be set free when the substance falls back into the more stable equilibrium of its previous condition, by processes of katabolism, or final decay.

- C^2 . In Development x is the vitalized protoplasm and other forms of the organized material basis of the organism; and y is the differentiation of cell, tissue and organ, or what, in general, is described by the term organization of the body of the organism.
- C^s . In Evolution x is the individual organism, at any particular moment of its existence, which lengthens out by processes of generation into a series of successive individuals; and y is variation, when a single individual is considered, or divergence, when the series is considered, of both form and function, and results in 'modification of characters' and 'origin of species.'

The genetic phenomena in these three categories form a series in which y of the first becomes x of the second, y of second becomes x of the third; and thus y of the third seems to be the direct outcome of the matter taken in and appropriated in the metabolic process at the beginning of the series. This inference would follow were it not for a second fact, viz.: that the first group of phenomena never (according to present knowledge) takes place except when the matter flows into a living organism. This fact proves that the matter, except for the action of the living organism, would not metabolize, but would be simply aggregated to the previous mass of the organism, in the same condition as when it met the organism Thus it becomes evident that metabolism is a function of the organism upon receiving the increment of inert matter; and going on to the second category we likewise discover that the organizing of the matter is a function of the living organism; and still further on it is evident that the variation and the divergence of characters in evolution are functions of living organisms alone.

In each case the phenomena are alike for like conditions of previous living organism, but they are unlike for like conditions of both the material medium and the material additions derived from without the organism. Hence it is proper to say that the determination of the genetic phenomena may be traced directly to a previous living organism, always present and active, and not to the conditions of the materials without at any particular moment of the process.

NATURE OF AN ORGANIC BODY.

This brings us to the consideration of another problem: What kind of a thing is this organic body which exhibits such genetic phenomena?

Tait tells us that "In the physical universe there are but two classes of things, matter and energy." He has further elaborated the proposition in the following words: "Energy, like matter, has been experimentally proved to be indestructible and uncreatable by man. It exists, therefore, altogether independently of human sense and human reason, though it is known to man solely by their aid."

Again, in the Newtonian formula we have the following proposition about matter in general, viz.: "Every body continues in its state of rest or of uniform motion in a straight line, except in so far as it is compelled by force to change that state." With these definitions in our minds, what answer can be given to the question: Is a living organism an inert body or mass of matter? and second: Is its integrity and individuality determined by a compelling force? In forming a reply we note the following particulars:

1. The matter of a living organism, as well as its form or configuration, is constantly undergoing change, while its integrity, identity and individuality persist.

- 2. The atomic matter which flows into the organism in metabolism suffers change, both molecular and in mass, without interfering with the continuous operation of the genetic phenomena of the organism as a whole.
- 3. The energy which is added to that of the organism by way of this acquired matter does not determine the course of the genetic phenomena, since, as has been said, the same matter behaves differently as it enters different organisms, and different matter is made to behave according to the law of the organism which it unites with.
- 4. The thing transmitted from parent to offspring, through which alone we are able to trace the determining power of the genetic phenomena in each case, cannot be matter alone, for matter is in itself inert; as Maxwell tells us: "We are acquainted with matter only as that which may have energy communicated to it from other matter, and which may, in its turn, communicate energy to other matter. Energy, on the other hand, we know only as that which in all natural phenomena is constantly passing from one portion of matter to another." ('Matter and Motion,' p. 165, 1878.)
- 5. Hence it follows that that which determines the individuality of the genetic phenomena of a living body, constitutes the integrity of the organism as distinct from a mass of matter, and preserves its identity through all the changes it undergoes, is energy, not matter.
- 6. A living organism physically behaves, not like an identical mass of matter, but like a stream of matter slowly entering and departing from the field of some continuous, identical form of energy. It behaves like a magnet, or a heated body, the phenomena exhibted by which are temporary and determined by what is called a particular form of energy resident for the time in the mass, and not determined by the particular materials, or arrangement of materials, of

which the body is composed. Whenever the non-living matter from outside enters the living organism it exhibits for the first time the vital phenomena, and when it passes out of the field of the organism these peculiar phenomena cease and are not set up again till the matter comes again into the field of a living organism. Thus the physicist explains the color of an opaque object, not as the property of the material body as such, but as a phenomenon produced by the reflection of light energy by the body. The matter has color only as illuminated from without by light energy.

A GENETIC FORM OF ENERGY.

This train of analysis leads to the recognition of a genetic form of energy, on the principle of classification used in physical science. The physicist already recognizes the three forms-chemical, molecular and molar en-The basis of that classification is the distinction between the three kinds of material units whose relation to each other, in each case, is disturbed in the phenomenal expression of energy of the several forms. Chemical energy is expressed when the relation of atoms changes. Molecular energy is the form of the energy when molecules change their relations; and it is molar energy which is exhibited when bodies or masses of matter change their positions in relation to each other. The genetic phenomena, above described, differ from the phenomena of each of the three classes named in that they concern changes of relation of living organic bodies only. It seems, therefore, appropriate, on this basis of classification, to speak of genetic energy as a fourth form of energy of equal rank with the chemical, molecular and molar energies of the physicist.

The recognition of this peculiarity of genetic energy gives at once rational meaning to such terms as doing, varying, acquiring, etc., which are appropriate when applied to organisms, but have only figurative meaning when applied to any other of the classes of matter or material bodies.

When a living organism is compared with a mechanical engine we note, first, that the work done by the machine is all accounted for by (a) the amount of coal burned and other potential energy entering in a similar way; and, second, that the construction (what Maxwell called the 'configuration of the mass') of the machine is accounted for by (b) the energy of the laborers expended in building it, together with (c) the potential energy of the bodies of matter used in the construction. But after balancing all these resources with the corresponding work accomplished, there still appears an item of cost of energy that has gone into the machine which must be represented also on the side of work done, viz.: (d) the designing of the architect.

Employing the same evidence which Tait deemed to be valid as a proof of the objective reality of energy, i. e., the price of labor, we discover that the architect's labor must be accounted for in the work done, else it was wasted energy. Furthermore, because, on the potential side of the account, we are able to sharply distinguish the designing from the constructing of the engine, we are authorized to reckon them as separate elements in the cost of the work done. It is to be noted that the particular kind of work performed by the architect, although it involves motion, is not strictly speaking any particular mode of motion, which may be measured in terms of horsepower, though measurable in terms of manpower. This may explain the reason why no account of his work is taken in estimating the potential energy of a machine. Nevertheless, all know that it requires the expenditure of energy which has a price, and is exerted only by a living organism.

If designing costs energy in the construction of a physical machine, is it not reasonable to look for a similar expenditure of energy in the construction of a living machine? In the phenomena of an organism we find the same groups of expenditure involved in the work done. These expenses are (a) the outside energy of heat, etc., of the food consumed; (b) the energy used in tissues exhausted in growth of construction; (c) that of the materials built into the structure with their potential energies abiding with them. These three. like the first three in machine construction, are accounted for on both sides of the equation. There remains to be considered the fourth group (d), viz.: that which corresponds to the designing of the machine and the potentiality of work consequent upon the designing. It will now be evident that, in the organism, that group of phenomena classified above as genetic constitutes this fourth group. The importance of, and the direction in which successful search for the source of genetic energy is likely to be made, are suggested by the following three First the chief aim of biological investigations for the last half century has centered about the search for exactly this determining cause of the particular form of construction of organisms. This, in itself, is sufficient evidence of a prevailing belief that some such cause is to be naturally accounted for. Secondly, the main points of construction of a particular organism correspond to those of the parent organism, and not to anything in the material of which it is constructed, is sufficient to suggest the direction from which the energy comes which determines the construction. third fact, that the three kinds of genetic phenomena (metabolism, development and evolution) are but elaborations of a single mode of operation, further points to the probability that the determining energy in question is the same for each. And all these considerations seem to lead directly to the conclusion, that some form of energy

must be predicated for the purely genetic phenomena of organisms, to account, that is, for the particular course of development followed by each species, and the particular course of divergence seen in each line of evolution. These conclusions seem to rest on as valid a foundation as that the visible colors of bodies are determined by light energy, or that the temperature phenomnena of physical bodies are determined by heat energy.

APPLICATION OF THE THEORY OF GENETIC ENERGY.

The application of this theory of genetic energy will become evident by attempting to distribute, in accordance with it, such a set of vital phenomena as are grouped together in Darwin's list of factors of evolution. In the 'Origin of Species' Darwin gave the following brief summary of the factors entering into the origin of species:

"These laws, taken in the largest sense, being growth, with reproduction; inheritance, which is almost implied by reproduction; variability, from the indirect and direct action of the external conditions of life, and from use and disuse; a ratio of increase so high as to lead to a struggle for life, and as a consequence natural selection, entailing divergence of characters and the extinction of less improved forms."

In this list eleven distinct factors are named. The question arises: What is the place of each in a system of vital phenomena in which variability is assumed to be the most fundamental of all?

The first factor, growth, in so far as it includes the material increase of the living body by the acquirement of matter from outside, and the reduction of it to a living state in metabolism, is one of the three forms of the fundamental genetic phenomena of variability.

The second factor, reproduction, is made up of two distinct phenomena: (a) the act

of separating a living body into two or more distinct units, precisely called generation; and (b) the process by which the individual body is constructed after the fashion of its immediate ancestors, precisely called development. (a) The first, generation, is a mechanical phenomenon, not necessary or fundamental to all living; for it is not continually occurring, nor is it possible to occur till after some degree of development is accomplished. Hence, we may assume that it is an acquired phenomenon, i. e., an expression of interaction between the genetic energy of the organism and the energies of the materials of construction and the environment. (b) The second, development, is the second form of the fundamental process above described, and is a necessary and universal characteristic of all living bodies. In Darwin's list the phenomena of development are partly included under the term growth, but material increase is not necessarily development. Metabolism is the acquirement and vivifying of inert matter by and into an individual organism; development is the differentiation of this mass into increased complexity of organization and function.

The third factor, inheritance, is the name for the law observed in the course of development by which the living body successively assumes the characters of the other body from which it was separated in gener-This law of repetition of the charters of ancestors cannot be a fundamental phenomena, because if it were strictly carried out no development would take place, and evolution results only by ignoring or transgressing the law of inheritance. must assume, therefore, that inheritance is acquired, and in any series of organisms the law of inheritance became operative only after generation had arisen, and after the attainment of some degree of inequality had been reached between parent and offspring at the point of the act of generation,

i. e., the parent organism must be more developed than the germ cell it propagates. Inheritance is the completing of the development of the germ as a separate body after generation in the likeness of the parent from which it was separated.

The fourth factor, variability, is the primary genetic phenomenon of all organisms which, in a particular case, relatively or entirely ceases with the acquirement of inheritance in the course of development, or with the acquirement of fixation and permanence of specific form in evolution. It may be regarded as the most direct and characteristic expression of genetic energy.

The next three factors, ratio of increase, struggle for life and natural selection, are, as vital phenomena, of a purely secondary nature. Each of them implies the previous operation in the same organism of development, variation and the acquired phenomenon of generation. The discussion of these factors, though of extreme interest for other purposes, and by many considered to be the chief causes of evolution, do not appear as true determining causes of modification, but causes rather of removal from the field of such organisms as cease to continue in the race. This point was granted by Darwin, as Cope reminded his readers in 'Primary Factors of Evolution.' held that natural selection does not induce variability; 'it implies only the preservation of such variations as arise and are beneficial.

In making this statement it is important to note the distinction between variability and variation. A variation which is transmitted or preserved by natural selection loses its variability exactly to the extent of its preservation; therefore, natural selection checks variability.

The factors of indirect and direct action of the external conditions of life, and use and disuse, which in the Darwinian and Lamarckian theories of evolu-

tion play so important a part as causes of variation, cannot hold their place of supreme importance if, as is here maintained, variation be the fundamental factor in genetic problems. From this latter point of view the organism is conceived of, not as passively shaped by the conditions of environment, but as finding its fundamental function in actively occupying environment; and adjustment is a positive active process involving constant modification. Adjustment is, thus, a result of successful varying, rather than varying a result of maladjustment. From this point of view the factors, external conditions of life, use and disuse, struggle for life, and natural selection, though operative in determining the course of developmental construction of the organism, are effective in the way of limiting, restricting, giving permanence to and making hereditary the characters which arise by the direct activity of genetic energy.

The tenth factor, divergence of characters, which by Darwin was conceived of as the direct result of the action of the above factors, is, according to this view, a characteristic genetic phenomenon, taking place with greater or less rate of progress in every organic series. It is organic evolution, proper, and consists in the acquirement, by a particular living organism, in the course of its individual development, of characters not possessed by its ancestors. The first step in such evolution is necessarily variation.

This analysis of the Darwinian factors of evolution presents us with two classes of phenomena, viz.:

I. Three of them are fundamental phenomena exhibited by every living organic body, and it would appear (although not always visibly, still theoretically) continuously during active existence of the organism. These have been called genetic phenomena, because they are constantly resulting in genesis of changed state, condition or

form of the bodies exhibiting them. They are: (a) Growth, strictly speaking Metabolism; (b) Development (the second part of the factor called Reproduction by Darwin), and (c) Divergence of Character—properly Evolution—which includes the phenomena of variation.

II. The second group of factors are all of a secondary nature. They are: (a) the first part of Reproduction, i. e. Generation, which is seen in its simplest form in Mitosis, next in cell-cleavage, in which the process results in producing two more or less equal and similar parts; and only in organism of some degree of differentiation in structure does it result in true generation through the formation of immature germ-cells, which continue development along hereditary lines of generation; (b) Inheritance, which cannot take place till inequality between germ and parent is already attained at the time of generation, and the attainment of this inequality cannot be primitive; (c)Ratio of Increase; (d) Struggle for life, and (e) Natural Selection, none of which can occur till after generation and inheritance have resulted in the production of antagonistic individuals.

The fundamental genetic phenomena of the first group are related to each other, and therefore distinguished, in the same way as the fundamental phenomena of nonliving matter are related and distinguished in chemical, molecular and molar groups. Metabolism pertains to changes in the molecular relations of the contents of a living cell; Development pertains to transmutations of the cellular contents (as cells, tissues and organs) of a living unit, i. e., the organic individual; Evolution pertains to the modifications of the individual members of a genetic series of successive organisms. These three forms of genetic phenomena are alike in that they all consist in the modification or change in the mode of action or function of the body expressing them.

In Metabolism, molecules, which in normal chemical phenomena (not organic) have been at rest, or passing into or toward conditions of more stable equilibrium, in vital phenomena pass upward into more unstable combinations. I speak, of course, of the anabolic phenomena of metabolism.

In Development, bodies, which under the influence of physical forces would move toward a state of greatest rest and equilibrium, are in the living body actively engaged in changing position and overcoming resisting forces.

In Evolution, series of bodies, normally revolving in adjusted cycles of generational reproduction are slowly departing from the hereditary course of these cycles, and acquire new characters which their ancestors did not possess.

The recognition of the fundamental nature of this principle of varying, or transmutation, in living bodies not only ties together all the vital phenomena into a consistent system of correlated processes, but it brings their phenomena into a natural relationship to the normal phenomena of inorganic matter.

The path by which these conclusions are reached is not a new one, but is simply an extension of the same line of thought which a century ago led to the overthrow of the Cuvierian notion of species. The mutability of species was a necessary preliminary step in the formation of a clear notion of organic evolution. We must carry the idea one step further and recognize the essential mutability of the organism. As in the last century the whole classification of organisms was based on the theory that the species was an immutable unit, so at the present time the whole classification of biological phenomena is based on the assumption that heredity is a fixed immutable law. The principle of mutability must be recognized in the phenomena of development before we can rightly comprehend the laws of organic life.

Variability is the expression of the fundamental energy of the organism, and is not an irregular accident. Heredity is the expression of the acquired adjustment of the organism to the conditions of its existence. Mutable heredity sounds like a contradiction; so did mutable species a century ago; but it is only as heredity is mutable that evolution is possible.

THE MEASUREMENT OF SMALL GASEOUS PRESSURES.*

Prior to the invention of the McLeod vacuum gauge, the measurement of even moderately small gaseous pressures was difficult, and subject to large errors. introduction of the McLeod gauge, however, early in the seventies, seemed to solve the problem. In its ordinary form, and for most purposes, this beautiful instrument admirably serves the purpose for which it is designed. But when very accurate measurements of pressures as small as a few millionths only of atmospheric pressure are desired, its performance is extremely unsatisfactory and vexatious. As is well known, the chief cause of the difficulty is the unequal and variable capillary depression of the two small columns of mercury. whose difference in height indirectly serves as the measure of pressure. Accurate measurement of this capricious difference obviously avails nothing.

Three or four years ago I was engaged in an investigation requiring frequent and simultaneous measurements of slight but different pressures in two large glass globes connected by a capillary tube. For this purpose I constructed and carefully calibrated two large McLeod gauges. The internal diameter of the mercury tubes was about three millimeters, and they were made from contiguous parts of the same glass tube selected for uniformity of bore.

* Read before the American Association for the Advancement of Science, August 12, 1897.

These gauges were often compared by measuring the same vacuum with both, but they rarely gave concordant results. Indeed, it was not uncommon at high exhaustions for one or the other of them to indicate a negative vacuum; that is to say, less than no pressure at all. The case of these two gauges is cited because of the opportunity they afforded for comparison. In prior work I had, like most experimentalists, used but one gauge, and, while always suspicious of its indications, had no means of knowing how large its errors might be.

The phenomenon which I next desired to investigate is the spontaneous evolution of of gas from glass and other surfaces in high vacua. For this purpose an accurate and entirely reliable means for measuring very small pressures was necessary, because I could not afford to wait months or years for the evolution of sufficient gas to be detected with certainty by the old gauges. To meet these requirements, I designed, constructed, and learned how to use, the modified form of McLeod gauge, which it is the purpose of this paper to discuss.

The diagram herewith shows the essential parts of my apparatus. The bulb A, of the gauge, is made conical in its upper part to avoid adhesion of gas bubbles when the mercury rises. This bulb holds about eleven pounds of mercury. B and C are the gauge head and comparison tube respectively. They are nearly twenty millimeters inside diameter, and are made from contiguous parts of the same carefully selected tube. D is the usual air trap, and E is a long glass tube, with flexible pure rubber connections to the lower end of the gauge stem and the mercury cistern F. The latter is mounted on a carriage G, which moves vertically on fixed guides. The height of the carriage is adjustable, at the upper end of its range of motion, by means of screw H, thumb-nut I and forked support K. The screw is pivoted to the